RESEARCH

Predicted Efficiency of Spaced-Plant Selection to Indirectly Improve Tall Fescue Sward Yield and Quality

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ABSTRACT

The validity of spaced-plant evaluation to determine sward performance of forage grasses has been questioned. This experiment studied the efficiency of spaced-plant evaluation to indirectly improve sward yield and nutritional quality in tall fescue (*Festuca arundinacea* Schreb.). Narrow-sense heritabilities, genetic and rank correlations, and indirect selection efficiencies were estimated for a tall fescue population grown in spaced plant and seeded sward environments. Heritability for yield was similar between spaced plants and swards (0.43 and 0.44, respectively), but genetic correlation between the two was low (0.37 ± 0.38). Inconsistency (r = 0.30, P = 0.17) in family ranking further suggested that spaced plants were not predictive of sward yield. Heritability of crude protein from swards was low (0.27 ± 0.25) compared with 0.77 ± 0.08 from spaced plants, but there was no genetic relationship between the two (r = −0.13 ± 0.30). Moderate to high heritabilities and genetic correlations were observed for most fiber traits, but indirect selection efficiencies and rank correlations of <1.0 suggested that evaluation in a sward environment would be best to select for improved nutritional quality. Spaced-plant evaluation appears to be less effective, or ineffective, at improving sward yield and nutritional quality in tall fescue. New techniques are needed that maximize genetic expression but simulate actual sward production of forage grasses.

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Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; CP, crude protein; dNDF, digestible neutral detergent fiber; HSF, half-sib families; IVTD, in vitro true digestibility; NDF, neutral detergent fiber.

Most forage breeding programs have used spaced-plant evaluation to select breeding materials; however, the ability of spaced plants to predict sward yield has been questioned (Casler et al., 1996). The lack of substantial genetic improvements in yields of smooth bromegrass (*Bromus inermis* Leyss.; Casler et al., 2000b), orchardgrass (*Dactylis glomerata* L.; Casler et al., 2000a), perennial ryegrass (*Lolium perenne* L.; Hayward and Vivero, 1984), and many other pasture grasses may be largely due to the lack of direct selection for forage yield on sward plots (Casler et al., 1996).

As early as the 1940s, it was reported that spaced plants were not predictive of the sward performance of white clover (*Trifolium repens* L.; Atwood and Garber, 1942) or Kentucky bluegrass (*Poa pratensis* L.; Ahlgren et al., 1945; Kramer, 1947). Since that time, low correlations, inconsistent rankings, and genotype × spacing interactions have been reported for forage yield between spaced plants and sward plots in orchardgrass (Knight, 1960; Oldemeyer and Hanson, 1955), perennial ryegrass (Hayward and Vivero, 1984; Lazenby and Rogers, 1964, 1965; Samuel et al., 1970; Wright, 1960), timothy (*Phleum pratense* L.; Nissen, 1960), smooth bromegrass (Carpenter and Casler, 1990; Grissom and Kalton, 1956), crested wheatgrass

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(Asay and Johnson, 1997), and alfalfa (*Medicago sativa* L.; Annicchiarico, 2006; Asay et al., 1999).

Other researchers have reported positive relationships between spaced-plant and sward evaluations, and have argued that spaced plants offer additional selection benefits to forage breeding programs. Lazenby (1957), Copeman and Swift (1966), and Humphreys (1989) all reported similar relative yield performance between spaced plants and swards of perennial ryegrass. Copeman and Swift (1966) went on to conclude that the greater variation observed among entries grown as spaced plants made selection using widely spaced plant nurseries preferable. Sedcole and Clements (1973) reported high genetic correlations and similar heritabilities for forage yield between 0.6- and 0.1-m spacing in *Lolium multiflorum* × *L. perenne* hybrids. They concluded that selection among widely spaced plants had been unduly criticized and that the ease of planting and maintaining spaced plants made this technique preferable in forage breeding. England (1975) surmised that in Italian ryegrass (*L. multiflorum* Lam.), a genetic correlation of 0.86 between swards and widely spaced plants, and a higher heritability from spaced-plant evaluation, made indirect selection for sward yield more efficient than selection for yield per se. Burton (1985) and Casler et al. (1997) both reported that selection for yield among spaced plants improved sward yield. Burton (1985) worked with a highly rhizomatous grass, however, and Casler et al. (1997) concluded that multilocation evaluation of spaced plants was critical for successful indirect selection.

As described, there is not consensus on the value of spaced plants in a forage yield improvement program. The majority of the literature suggests that indirect selection using spaced plants will not result in increased sward yield, and in fact the two options may be under different genetic controls, but even after decades of reports there is a noticeable lack of novel or modified procedures in forage breeding. The role of spaced plants vs. swards in tall fescue (*Festuca arundinacea* Schreb.) breeding has not been reported. The objective of this study was to compare genetic parameters and the efficiency of indirect selection using spaced plants to improve sward yield and nutritional quality in tall fescue.

MATERIALS AND METHODS

Plant Materials and Evaluation

In 2001, 22 half-sib families of tall fescue were established in adjacent evaluation nurseries, one consisting of widely spaced plants and the other being seeded swards. The spaced plant nursery was considered representative of a "selection environment;" whereas seeded swards represented the "production environment." The 22 half-sib families were developed via an earlier polycross of 22 plants selected from a large broad-based Cycle-1 evaluation nursery. The experimental plots were established at the Utah State University Evans Research Farm, approximately 2 km south of Logan, UT (41°45′ N, 111°8′ W, 1350 m above sea level). Soil type at this site is a Nibley silty clay loam series (fine, mixed, active, mesic Aquic Argixeroll).

The spaced-plant environment was established in August of 2001 by transplanting greenhouse-started seedlings to the field in 10-plant plots with 0.5 m between plants and 1 m between rows. The seedlings were started in the greenhouse during the winter by germinating grass seeds in blotter trays and then transplanting germinated seeds into individual cells (Ray Leach Cone-tainer SC-10 Super Cells [21 cm deep, 4 cm diam.], Stuewe and Sons, Corvallis, OR) containing a 3:1 soil/peat mix, where they were grown until transplanting to the field. The sward environment was established 6 Sept. 2001 via drilling sward plots using a Wintersteiger cone seeder (Wintersteiger Corp., Salt Lake City, UT) at a seeding rate of 135 pure live seed per linear meter of row. Plots were 3 m long, consisting of six drilled rows 18 cm apart. Field design for both spaced-plant and sward environments was a randomized complete block design with four replicates. Both environments were irrigated weekly, receiving 3.8 cm water wk^{-1} (approximately 100% season-long evapotranspiration replacement), and fertilized with 56 kg N ha^{-1} after the first, third, and final harvests.

Individual plots from each environment were harvested with a sickle-bar mower to an 8-cm stubble height when growth in the swards was at the boot stage of plant development for the first harvest and when the height of regrowth was approximately 35 to 40 cm for subsequent harvests. Plots were harvested on 13 May, 5 June, 3 July, 24 July, 21 Aug., and 26 Sept. 2002, and 22 May, 19 June, 18 July, 21 Aug., and 2 Oct. 2003. Forage samples were taken from each plot and dried to a constant weight in a forced-air oven at 60°C to determine dry matter percentage. In addition, plots were visually evaluated or measured on 1 July 2002 and 3 July 2003 for height, tiller density, and leaf softness.

Dried forage samples from the July harvests in 2002 and 2003 were double ground with a Wiley and Cyclone mill to pass through a 1-mm screen, and scanned with a Model 6500 near infrared reflectance spectroscopy (NIRS) instrument (Pacific Scientific Instruments, Silver Spring, MD). NIRSystems software was used to calibrate existing equations so that they were appropriate for this study. Random samples were selected from each year and used as a calibration data set for wet laboratory analyses. Validations of the new equations were determined from a different set of duplicate samples for crude protein (CP) (N × 6.25), neutral detergent fiber (NDF), digestible NDF (dNDF), acid detergent fiber (ADF), acid detergent lignin (ADL), and in vitro true digestibility (IVTD). The *r* values for validation computed across years were 0.99 for CP, 0.85 for NDF, 0.72 for dNDF, 0.79 for ADF, 0.84 for ADL, and 0.81 for IVTD. Samples used for calibration were analyzed for N using a LECO CHN-2000 Series Elemental Analyzer (LECO Corp., St. Joseph, MI). Neutral detergent fiber, ADF, ADL, and IVTD were determined following the methods of Goering and Van Soest (1970) as modified in the ANKOM procedures (Ankom Technology, 2005a,b,c,d). The first stage of the IVTD procedure consisted of a 48-h in vitro fermentation in the ANKOM Daisy II incubator (ANKOM Technology Corp., Macedon, NY). Analyses for NDF, ADF, and for the second stage of the IVTD procedure were made with an ANKOM-200 Fiber Analzyer (ANKOM Technology Corp.).

The IVTD procedure differs from the classic two-stage Tilley and Terry in vitro dry matter digestibility procedure by substituting an NDF extraction for pepsin and HCl in the second stage. This results in a more complete removal of bacterial residues and other pepsin-insoluble material and generally results in a higher digestibility value. Digestible NDF values were calculated using the initial concentrations of NDF and IVTD.

Statistical and Genetic Analysis

Data were analyzed within environment (spaced plant vs. seeded sward) across years using the MIXED procedure of SAS (SAS Institute, 1999) and a split plot in time design (Nguyen and Sleper, 1983). Half-sib families (HSF) and years were considered to be random.

The indirect response in sward performance that would result from selection in the spaced-plant environment was predicted using the correlated response theory and equations described by Falconer (1989, p. 324) and reviewed by Burdon (1977) and Cooper et al. (1993). Briefly, these studies validated that the underlying basis for correlated response to selection between traits can be extended to the correlated response between the same trait measured in two environments. This approach has been widely used to evaluate indirect selection response between breeding vs. target environments, including high-yield vs. low-yield environments, and laboratory or greenhouse evaluation vs. field environments (Atlin and Frey, 1990; Burdon, 1977; Ceccarelli et al., 1992; Cooper et al., 1993; Stratton and Ohm, 1989; Waldron et al., 1998). Additive genetic variances (σ^2_A), narrow-sense heritabilities, and genetic correlations were estimated assuming the variance among HSF was equivalent to ¼ σ^2_A. Narrow-sense heritabilities and standard errors were calculated within the spaced-plant and sward environments based on HSF means of a perennial species evaluated at one location for multiple years using the SAS code described by Holland et al. (2003). Additive genetic correlations between spaced plant and sward environments were estimated as

$$r_{G(\text{spaced,sward})i} = \sigma_{G(\text{spaced,sward})i} \Big/ \left[\sigma_{G(\text{spaced})i}\sigma_{G(\text{sward})i}\right]$$

where $r_{G(\text{spaced,sward})}$ is the genetic correlation that measures the association at the HSF level of trait *i* in a spaced-plant and sward environment, $\sigma_{G(\text{spaced,sward})}$ is the additive genetic covariance of HSF means for trait *i* when evaluated in spaced-plant and sward environments, and $\sigma_{G(\text{spaced})}$ and $\sigma_{G(\text{sward})}$ are the square roots of the additive genetic variances for trait *i* when evaluated in a spaced-plant or sward environment, respectively. Additive genetic variances and covariances were estimated with method of moments procedures using mean squares and mean cross products according to Via (1984, Method 2). Mean squares and mean cross products were obtained from the GLM procedure of SAS (SAS Institute, 1999). Approximate standard errors of genetic correlations were calculated according to Falconer (1989, p. 317).

The expected efficiency of indirect selection (e.g., family selection within a spaced-plant environment to increase sward yield) was calculated as the ratio of correlated response (CR) to direct response (*R*) as

$$\begin{aligned}\text{Efficiency}_{\text{indirect selection}} &= \text{CR}_{\text{sward}} / R_{\text{sward}} \\ &= i_{\text{spaced}} h_{\text{spaced}} r_{G(\text{spaced,sward})} / i_{\text{sward}} h_{\text{sward}}\end{aligned}$$

where i_{spaced} and i_{sward} are the selection intensities in a spaced-plant and sward environment, respectively, h_{spaced} and h_{sward} are the square root of the heritabilities of a trait in a spaced-plant and sward environment, respectively, and $r_{G(\text{spaced,sward})}$ is the genetic correlation between the spaced-plant and sward environments for any given trait (as defined above) (Falconer, 1989). In this study, i_{spaced} and i_{sward} were considered equal, thus any ratio <1.0 indicated that indirect selection was less efficient than direct selection. Spearman's rank correlations and "correct" and "erroneous" selections were determined as additional estimates of relative breeding value of the spaced-plant environment to indirectly improve sward performance. Correct selections were defined as the best six HSF (top 27%), and erroneous selections were the bottom six (27%) HSF as determined from the sward environment. A counting was made on the number of correct and erroneous selections in the top six HSF as ranked by spaced-plant evaluation.

RESULTS AND DISCUSSION

Spaced vs. Swards: Mean Performance Comparison

Overall means for each trait as grown in spaced-plant and sward environments are listed in Table 1. Mean values for most traits differed between the two environments, with the exception of height, tiller density, and ADL (Table 1). Forage yield on a per-unit-area basis was >200% higher for the sward than spaced plants. This is comparable to the results of Lazenby and Rogers (1964) where perennial ryegrass grown in swards more than doubled the yield of spaced-plant plots on 0.7-m centers. Sward plots had stiffer leaves and lower nutritional quality as measured by CP, NDF, dNDF, ADF, and IVTD than that found in the spaced-plant environment (Table 1). Lazenby and Rogers (1965) also found that N (as a measure of CP) was always higher from perennial ryegrass spaced plants (0.6-m centers) as opposed to those grown in swards. And, like our results, their (Lazenby and Rogers, 1965) crude fiber was also higher in sward plots; however, their fiber measurements were reported on a unit-area basis and therefore did not directly relate to our dry matter basis. In contrast, Humphreys (1989) reported lower yields, higher digestibility, and mostly higher CP for sward plots of perennial ryegrass compared with spaced plants. Unlike our study and those of Lazenby and Rogers (1964, 1965), however, Humphreys used an unequal number of cuttings between the two environments. The three additional cuttings (within the growing season) of the sward plots resulted in less-mature regrowth, and probably explains these differences, especially the higher digestibility and CP.

Spaced vs. Swards: Heritability, Rank, and Selection Comparison

Genetic correlation estimates usually have large sampling errors and are seldom very precise, but are usually still indicative of expected correlated response to selection

Table 1. Mean values for forage yield and morphological and nutritional quality traits of tall fescue measured in spaced-plant and sward environments.

Trait†	Spaced	Sward	Probability of difference
Yield and morphological			
Forage yield, kg dry matter ha^{-1}	7376.8	16211.0	<0.0001
Height, cm	38.8	38.0	0.0519
Tiller density (visual; 1–9, 9 = dense tillers)	6.3	6.1	0.1158
Leaf softness (visual; 1–9, 9 = soft lax leaves)	5.7	5.1	0.0008
Nutritional quality			
Crude protein, g kg^{-1} dry matter	188.2	157.3	<0.0001
Neutral detergent fiber, g kg^{-1} dry matter	488.9	498.0	<0.0001
Digestible neutral detergent fiber, g kg^{-1} dry matter	647.3	610.8	<0.0001
Acid detergent fiber, g kg^{-1} dry matter	323.6	331.7	<0.0001
Acid detergent lignin, g kg^{-1} dry matter	81.7	81.6	0.9245
In vitro true digestibility, g kg^{-1} dry matter	822.2	803.5	<0.0001

†Trait values were determined by evaluating 22 half-sib families during 2001 and 2002 near Logan, UT. Nutritional values are from the early July harvest of a multiharvest system.

(Falconer, 1989). We observed that the genetic correlations for forage yield and crude protein were not greater than 1.96 times their respective standard errors, suggesting that these correlations were not significantly different than zero (Table 2). Even so, we used the absolute correlation value for these traits in calculating indirect selection efficiency. Conclusions concerning indirect selection for these traits were made with caution only after comparing the genetic correlation with the Spearman's rank correlation and the number of correct or erroneous selections. In addition, genotype × plot area interactions may have biased genetic correlations; however, this confounding was minimized by independent randomization within each environment (Nguyen and Sleper, 1983), and high macroplot uniformity as observed by the researchers from multiple previous studies at this location.

Forage Yield and Morphological Traits

Heritable variation for forage yield was similar between spaced plants and swards, with h^2 of 0.43 and 0.44, respectively. The resulting genetic correlation was low (r_G = 0.37 ± 38), however; consequently indirect selection for forage yield using spaced plants was much less efficient (efficiency = 0.37) than direct selection of sward yield per se (Table 2). A nonsignificant Spearman's rank correlation suggested a lack of agreement in yield rank between the two environments, and examining the number of correct selections indicated that only 50% of selected parental lines were in common between the sward and spaced-plant environments (Table 2). The similar values between selection efficiency and correct selections highly suggests that gains in breeding for sward forage yield will be minimal or highly reduced when selection is based on spaced-plant evaluation.

We found that there was no heritable variation for plant height in the spaced-plant environment (h^2 = 0.14 ± 0.37), whereas height was moderately heritable (h^2 = 0.53 ± 0.16) in the sward environment (Table 2). Thus, even though there was a high genetic correlation between the environments (r_G = 0.85 ± 0.25), spaced-plant selection will not change the height of swards (Table 2). This difference was further validated by a nonsignificant Spearman's rank correlation, and two erroneous selections resulting from spaced-plant evaluation (Table 2). The efficiency of indirect selection using a spaced-plant environment approached 1.0 (efficiency = 0.77) for tiller density, due to a moderate genetic correlation and higher heritability among spaced plants vs. swards (Table 2). Again, however, there was no relationship in family ranking between spaced-plant and sward environments (r = 0.19, not significant), with two correct and one erroneous selection using spaced-plant evaluation (Table 2). These results suggest that spaced-plant evaluation of height and tiller density (to a lesser degree) is not predictive of these same traits in a sward.

In contrast, we did observe high genetic and significant rank correlations between the two environments for leaf softness (Table 2). Indirect selection was still less efficient than selection in a sward (efficiency = 0.83), however, due to the lower heritability of spaced-plant evaluation. Four correct selections out of a possible of six validated a selection efficiency that approached 1.0, but one erroneous selection further indicated that direct selection in swards would more rapidly increase leaf softness.

Results from this tall fescue study seem to confirm that indirect selection using spaced plants for yield and related morphological traits does not translate to similar gains when these selections are grown in grass swards. Approximately 60 yr ago, researchers reported that productivity of individual Kentucky bluegrass plants had little relationship with seeded plots (Ahlgren et al., 1945; Kramer, 1947). Nissen (1960) reported the inability to predict timothy sward hay yields from spaced-plant evaluation. Samuel et al. (1970) found that perennial ryegrass cultivar rank was completely reversed between sward and spaced-plant (0.7-m centers) evaluation. Lazenby and Rogers (1964) reported similar findings in perennial ryegrass; however, they did find that plants grown at 23- or 8-cm-center spacing were predictive of sward yield. It is also interesting to note that spaced-plant evaluation was not predictive of combining ability for sward forage yield of smooth bromegrass (Grissom and Kalton, 1956) or orchardgrass clones (Oldemeyer and Hanson, 1955). More recently, Asay and Johnson (1997) concluded that, due to entry × spacing interactions, crested wheatgrass screening should be done using spacing realistic of actual rangeland conditions.

Table 2. Heritability (h^2), genetic (r_G) and Spearman's rank ($r_{Spearman}$) correlation estimates,† efficiency of indirect selection ($E_{indirect}$), and number of "correct" and "erroneous" selections (six possible each) from indirect selection for forage yield and morphological and nutritional quality traits of tall fescue measured in spaced-plant and sward environments.

Trait‡	h^2_{spaced}	h^2_{sward}	$r_{G(spaced,sward)}$§	$E_{indirect}$¶	$r_{Spearman}$	Selections#	
						Correct	Erroneous
						no.	
Yield and morphological							
Forage yield	0.43 ± 0.19	0.44 ± 0.19	0.37 ± 0.38	0.37	0.30 NS††	3	0
Height	0.14 ± 0.37	0.53 ± 0.16	0.85 ± 0.25	0.44	–0.08 NS	0	2
Tiller density	0.49 ± 0.22	0.37 ± 0.21	0.67 ± 0.28	0.77	0.19 NS	2	1
Leaf softness	0.33 ± 0.22	0.59 ± 0.14	1.11 ± 0.09	0.83	0.62*	4	1
Nutritional quality							
Crude protein	0.77 ± 0.08	0.27 ± 0.25	–0.13 ± 0.30	–0.22	–0.26 NS	0	1
Neutral detergent fiber	0.55 ± 0.20	0.44 ± 0.19	0.56 ± 0.27	0.63	0.22 NS	3	0
Digestible neutral detergent fiber	0.58 ± 0.14	0.61 ± 0.17	0.68 ± 0.14	0.66	0.31 NS	2	0
Acid detergent fiber	0.63 ± 0.12	0.30 ± 0.24	0.70 ± 0.20	1.01	0.23 NS	2	3
Acid detergent lignin	0.49 ± 0.22	0.56 ± 0.15	0.78 ± 0.13	0.73	0.54**	3	0
In vitro true digestibility	0.76 ± 0.08	0.72 ± 0.12	0.74 ± 0.07	0.76	0.49*	4	1

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

†All heritability and correlation estimates and standard errors are shown. Caution should be used in interpretation of values with large standard errors.

‡Trait values were determined by evaluating 22 half-sib families during 2001 and 2002 near Logan, UT. Nutritional values are from the early July harvest of a multi-harvest system.

§Genetic correlation between spaced plant and sward evaluation.

¶Efficiency of indirectly selecting for sward traits using spaced plant evaluation.

#Number of correct selections is determined by counting half-sib families indirectly selected using spaced-plant data that are in common with those selected from sward evaluation (top 27%, n = 6 possible); number of erroneous selections is determined by counting indirectly selected half-sib families (spaced-plant evaluation) that are in the bottom 27% of sward rankings.

††NS, not significantly greater than zero.

Hayward and Vivero (1984) reported that there was no relationship ($r = -0.01$) for yield between sward plots and 0.6-m spaced plants of perennial ryegrass. They surmised that their previous selection using spaced plants was equivalent to selection in a "good environment," and that due to genotype × environment interaction, the selected lines did not respond in the same manner when grown in the competitive "poor environment" of swards. They further suggested that these two different yield responses might be under the control of different genetic systems. Our results and conditions were very similar in that this tall fescue population had previously undergone selection via spaced-plant evaluation. Because we found similar heritabilities (e.g., relative within-population genetic variation) between the two environments, but a lack of genetic or rank correlation, we might make the same assumption that there are two different genetic controls for forage yield in this tall fescue population. Knight (1960) found very little relationship between spaced plants and swards in orchardgrass and suggested that limited moisture, light, and nutrients would result in a genotype × spacing interaction. Our study was conducted using an irrigation regime typical for the region, thus reducing the effect of moisture; but undoubtedly, on a plant-for-plant basis, spaced plants had greater access to moisture, light, and nutrients. Using path coefficient analysis, Voigt and Brown (1969) investigated the effect of seedlings per plot on forage yield of side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.]. They found that forage yield was affected only when seedling numbers differed greatly between plots and concluded that yield should be evaluated using seeded plots. The fact that spaced plants vs. swards are the extreme in terms of seedlings per plot further suggests that separate genetic responses occur as a result of resource competition.

Nutritional Quality

In general, for both spaced and sward environments, we observed moderate to high heritabilities for nutritional quality, and for the most part heritabilities were comparable between spaced plants and swards (Table 2). This is probably in part because this population had not undergone any selection, as spaced plants or swards, for any of the nutritional traits, as opposed to the previous selection for increased yield and softer leaves. A notable exception was CP, with a very high heritability from spaced plants (0.77 ± 0.08) and a low heritability from sward evaluation (0.27 ± 0.25), suggesting that indirect selection of spaced plants may be best. Genetic and rank correlations for CP were not significant, however, and were negative in nature, resulting in a negative value (−0.22) for indirect selection efficiency (Table 2). This was further validated by zero correct and one erroneous parent selection using spaced-plant evaluation (Table 2). It is reasonable that competition for soil N would result in a different genetic response for CP in competitive swards vs. the less competitive conditions of spaced plants; however, previous reports have been contradictory. In perennial ryegrass, Humphreys (1989) reported inconsistent CP levels between spaced-plant and seeded-plot evaluation, whereas Lazenby and Rogers (1965) found nearly identical ranking between 0.7-m spaced plants and pseudo-swards of 8-cm-center spaced plants. Our results are in agreement with Humphreys (1989), but the conflicting report by Lazenby and Rogers (1965) suggests that additional research is needed.

Moderate to high genetic correlations between spaced and sward environments were evident for NDF, dNDF, and ADF and corresponded to indirect selection efficiencies that ranged from 0.63 to 1.01 (Table 2). Even so, Spearman's rank correlations were not significant for these measures of fiber. Selection based on spaced plants would have resulted in 50% correct choices for NDF, but alarmingly would have resulted in three erroneous selections for ADF, even though spaced-plant evaluation was estimated to be equally efficient as sward selection (Table 2). The low heritability (and high standard error of heritability) of ADF from sward evaluation ($h^2 = 0.30 \pm 0.24$), however, undoubtedly caused discrepancies in what was classified as "correct" and "erroneous" selections.

The genetic relationships between spaced-plant and sward environments were high for ADL and IVTD (0.78 $\pm$ 0.13 and 0.72 $\pm$ 0.07, respectively). Even with the high genetic correlations, indirect selection efficiencies of spaced-plant evaluation approached but did not reach 1.0 because of higher or equivalent heritabilities for these traits under sward evaluation. Even so, ADL and IVTD were two of the few traits with a combined high genetic correlation, significant Spearman's rank correlation, and three or four correct selections resulting from spaced-plant evaluation (Table 2). Overall, these results suggest that spaced-plant evaluation would not be as effective as direct selection from sward environments but would still result in reduced lignin and increased digestibility.

Other researchers have reported consistent ranking between spaced-plant and sward environments with the potential to indirectly improve sward fiber content and digestibility via spaced-plant evaluation in perennial ryegrass and smooth bromegrass (Carpenter and Casler, 1990; Humphreys, 1989; Lazenby and Rogers, 1965). Our results suggest that direct selection via sward evaluation is more efficient, and would result in faster gains; however, our conclusions are based on equal selection intensity (*i*) for both spaced-plant and sward evaluation. Casler et al. (2002) reported that spaced-plant evaluation can accommodate screening many individuals compared with the relatively smaller number of families that can be evaluated in seeded plots. Thus high selection intensities, as well as increased use of additive genetic variance, is possible via selection of best plants within the best families. Under such an assumption, efficiency calculations may have favored spaced-plant evaluation to improve fiber and digestibility traits. As pointed out by Vogel and Pedersen (1993), however, to reduce evaluation costs it is common practice in grass breeding to first determine the best families (via family evaluation) and then afterward to determine the best plants within those selected families (via subsequent individual plant evaluation). In such a case, the equal selection intensity between the spaced and sward environments is realistic for family selection in a forage breeding program. Overall, our results suggest that spaced-plant evaluation will be moderately predictive of fiber and digestibility in a sward environment.

We conclude that indirect selection using spaced-plant evaluation will be less effective (possibly ineffective) at improving sward yield and CP, and only moderately predictive of sward leaf softness and some fiber and digestibility traits in tall fescue. While this is the first report of this kind in tall fescue, our results are in agreement with many other cool-season grass studies dating back as far as the 1940s. One must wonder about the continued predominant use in grass breeding of spaced-plant nurseries to predict yield and nutritional quality. One explanation is that the experience of many forage breeders has been that there is greater variation observed among families when grown in spaced-plant nurseries. Indeed, Copeman and Swift (1966) hypothesized that the greater variation within spaced-plant evaluation would ensure the development of the most productive cultivars. If these cultivars do not have improved performance under real-world sward conditions, however, then what was the value of the "greater variation"? New research is needed to streamline forage breeding by finding evaluation conditions that maximize genetic expression but are still predictive of actual sward production.

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